

in *Protea*, are very much reduced and form a dense column in the middle of the blossom, the main optical attractant of which is formed by the involucre. Also here there is a gradual development from the rather insignificant involucre in *L. argenteum* towards the more prominent one of most species. The aberrant male inflorescences of *L. plumosum* have been mentioned already. It must remain undecided whether they represent a primary primitive condition, or a secondary development.

Unfortunately, little is known about the pollination of *Proteaceae*, but a few points are known. Even to the most casual observer ornithophily is obvious, and already in the more primitive anthocladia of *Mimetes* the ornithophilous syndrome is clear: the small lateral inflorescences form brush blossoms of a very regular type. Bird visits have been recorded by Marloth (1901). The contrast between the primitive shoot morphology and the extreme specialization of the inflorescences is indeed striking.

No information seems to be available concerning pollination in *Faurea* and similar genera. The syndrome indicates entomophily. On the other hand, it is reported by seedsmen and breeders that birds are very important pollinators of the loosely organized heads of *Leucospermum*. According to available information the crop of *Leucospermum* seed is directly dependent on the frequency of pollinating birds during the flowering season. However, these brush blossoms are also visited by many other animals, of which the smaller, e.g. hive bees, seem to be able to reach the nectar without making contact with the stigmas (observed along the road near Stellenbosch). They must therefore be considered nectar thieves. But a large, green beetle, *Trichostetha fascicularis* which is known to visit these blossoms (observed in Kirstenbosch gardens), undoubtedly brushes against both stigmas and anthers when it lands on the heads, and probably also pollinates the inflorescences, even if a direct proof has not been given.

Birds are very active feeders in *Protea* blossoms and there is no doubt that they are also important pollinators. According to information, the long-tailed sugarbird, *Promerops cafer*, usually nests in *Protea* bushes and also takes practically all its nourishment from them. The narrow inflorescences of, e.g., *P. repens* (*P. mellifera*) are hardly negotiable by larger insects which would find great difficulty in entering between the massed styles. On the other hand the stiff involucral bracts certainly form very suitable perches for pollinating birds whose beaks reach the bottom of the inflorescence. As to the quantity of nectar available, the synonym as well as its popular name, "sugarbush", are sufficiently indicative. Observations show that *P. repens* is pollinated by birds.

When it comes to the open, bowl-shaped *Protea* blossoms, of which *P. cynaroides* has been quoted as an example, it is evident that they can be utilized by many nectar and pollen collecting animals. They are visited by birds, bees,

and beetles alike, and as their seed-setting (always irregular) is reported not to show such a close correlation to the occurrence of sugar-birds as in *Leucospermum*, it is not improbable that other groups are, at any rate partly, effective as pollinators.

In *Leucadendron*, the organisation of the blossom indicates that the pollinator should be short-tongued animals. Apparently, the black beetles *Genuchus hottentottus* (observed on Table Mountain), is an effective pollinator of these blossoms. To which extent they are also visited by other insects is unknown: the beetle, on its part, is not restricted to *Leucadendron*, but was also seen in other blossoms of a corresponding organisation (e.g. *Clutia*).

Within *Proteaceae* there is thus a "retrograde" development of pollination syndromes from the brush blossom type back to the more primitive bowl-shaped one concomitant with the progressive morphological development of the blossom. This development is apparently accompanied by a similar "retrograde" development amongst the pollinators, from pure or predominating ornithophily back to the assumed most primitive stage of cantharophily.

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STUDIES IN CYPERACEAE IN SOUTHERN AFRICA: I

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ABSTRACT

Studies in Cyperaceae in Southern Africa were undertaken in order to obtain information that might lead to more unified treatment of the sedges of Africa than exist at present, and that might eventually aid in clarification of the many taxa that are both African and world-wide, or pantropic, in distribution. Natural classification of Cyperaceae is essential if, eventually, generic relationships are to be more correctly appreciated and better understanding of infra and inter-tribal relationships achieved. A review of relevant literature is given.

GENERAL INTRODUCTION

The study of Cyperaceae in Southern Africa was undertaken as a direct consequence of difficulties met with in naming sedges collected during the course of ecological studies.

In Natal, situated on the warm south eastern coast of Africa and with a range of habitats from coastal to high mountain, many species are available for field study.

Prominent are representatives of predominantly tropical genera, numbers of which reach the limit of their southern distribution in Africa, either in Natal, or in adjacent areas of the eastern Cape Province.

Represented also, particularly at higher altitudes on the mountains, are species of predominantly temperate genera that may be regarded as outliers of the Cape Flora (Levyns, 1964). Natal is thus conveniently situated as the centre for such studies.

It was thought probable that in undertaking investigations throughout southern Africa, facts concerning morphological variation, ecological preferences and distribution might lead to better understanding of relationships between tropical and southern African taxa and those of Africa and the rest of the world.

Within Cyperaceae, generic limits are by no means always clearly defined nor stabilised, nor are phylogenetic relationships fully understood. Detailed studies are thus also necessary if, eventually, generic limits are to be more correctly established and better appreciation of infra- and inter-tribal relationships achieved.

REVIEW OF THE LITERATURE

The first publications devoted exclusively to the Cyperaceae of Southern Africa appear to be the accounts by Nees von Esenbeck (Nees 1832; 1833; 1836)

of the sedges collected by Ecklon. In the same year as the earliest of these, Schrader (1832) produced Part I, Cyperaceae, of his *Analecta ad Flora Capensem*, a small work in which forty nine species were described and twenty one figured. Kunth (1837) included a large number of Cyperaceae from Southern Africa in his systematic treatment of all the then known Monocotyledons. Of this work Bentham (1881) wrote, "... his monograph, forming the second volume of his *Enumeratio Plantarum*, is very much to be relied upon in everything that he states on his own authority. His chief errors are sometimes a tendency ... to give as characters rather what in theory we ought to see rather than what we actually do see, and ... to describe specimens rather than species".

Von Schlechtendal (1840) discussed the species of *Carex* in Schulte's edition of Thunberg's *Flora Capensis*. Steudel (1855) described many Southern African species, but did not limit his work to the sedges of this sub-continent. He was rather severely criticised by Bentham (l.c.) in the following comment, "Steudel came next with his *Synopsis Plantarum Glumacearum* which would have been a very useful work if he had had any idea of what constitutes a species or a genus. Wherever he could not readily determine a specimen he had before him, he at once described it as new, thus adding in no small degree to such confusion as Nees and others may have created".

In the period from 1855 to 1867 no major contributions to the knowledge of Southern African Cyperaceae were made. Some additional descriptions based for the most part on material collected by Drège appeared, but these were not many. The following ten years were important however, for it was during this time that Boeckeler (1867-1877) completed his survey of the Cyperaceae represented in the Royal Herbaria of Berlin and of other collections lent him for this purpose. This survey embraced almost every Southern African sedge then known. Boeckeler, according to Bentham, (l.c.) "... has verified a number of synonyms, and often successfully rearranged some of the species of the larger genera. His labours, however, would have been much more useful if he had had access to more of the works where Cyperaceae had been described; if he had not indulged so much in page-long uncontrasted diagnoses, if he had had rather a clearer idea of the principles upon which generic and ordinal distinctions are founded, and if he had adopted a more correct terminology."

There followed a further barren period which terminated with the publication of Vol. V, Monocotyledons, of Durand and Schinz's *Conspectus Florae Africae*. In this, the listing by Clarke (1895) of all the known African Cyperaceae, together with synonyms and the citation of specimens, was a considerable step towards a broad appreciation of the sedges of Southern Africa. In the light of more recent knowledge the work is not without errors, particularly those relating to the delimitation of species, but it is still a valuable reference.

Clarke was to make further extremely important contributions to the

literature in the years that followed. His account (Clarke, 1898) of the species of South Africa, with its detailed descriptions, notes on distribution, keys to identification and the citation of specimens, is still the most reliable guide available to those attempting to know the Cyperaceae of this region. Mention must also be made of his treatment (Clarke, 1902) of the Tropical African representatives of the family. Although only four years separated the publication of these two works, it seems Clarke did not consider the species of both regions conjointly so that some relationships that might have been obvious had he done this, escaped him.

Clarke's contributions culminated in the publication two years after his death, of part of his manuscript notes of a monograph on Cyperaceae he had prepared (Clarke, 1908). Here were included descriptions of several new southern African sedges, while all others were listed in relation to their allies among world species. One year later, illustrations prepared by several artists under Clarke's direction to supplement the text of his monograph were published (Clarke, 1909). Appreciation must be expressed of this botanist's considerable knowledge of this varied and difficult family and of problems relating to its classification.

It is fitting at this stage to mention a second botanist who, during his lifetime, also contributed greatly to knowledge of world Cyperaceae, including in his studies many African species. This was Kükenthal whose monograph on world Caricoideae was published in Engler's *Pflanzenreich* (Kükenthal, 1909).

In the field of anatomical structure which, in certain families, aids in the elucidation of phylogenetic relationships, little has been done concerning the Southern African sedges. Plowman (1906) in his paper based largely on American species, dealt with the internal structure of the family as a whole. Despite its quality, this work did little to stimulate research on African material. Only two papers are known in which contributions to this field of study were made. Gibbs (1908) dealt mainly with the anatomy of *Fuirena oedipus* C.B.Cl., a Rhodesian species. Pfeiffer (1920) included with notes on floral structure, distribution and groupings of species and citations of specimens, a short account of the anatomy of *Ficinia* Schrad.

Two years later, Schonland's (1922) *Introduction to South African Cyperaceae* appeared. This added little to information already available. By selection of usually only a single species from each section of a genus, Schonland avoided the problem of differentiating among very closely related taxa. It is perhaps doubtful whether he realised fully the closeness of specific relationships within some of the genera, for in his citation of specimens, he propagated errors made originally by Clarke. No keys were included. During the preparation of this work, Schonland sent many specimens to Kew for identification or confirmar-

tion. He suggested several new species that were subsequently described, together with other new South African species, by Turrill (1925).

Brain, (1934) produced *A Key to the Sedges of Southern Rhodesia*. Although including useful ecological and distributional information, photographs and figures, this paper is neither complete systematically, nor without inaccuracies.

Twenty seven years after his first monograph, Kükenthal (1936) made his second great contribution to world knowledge of the sedges, by the publication of his comprehensive account of Cyperaceae. Here were included descriptions, distributional notes and citations of African species of *Cyperus* L., probably the most commonly represented genus throughout the continent. Because of probable phylogenetic relationships and difficulties in clearly delimiting genera, Kükenthal included in *Cyperus*, *Juncellus* C.B.Cl., *Pycneus* Beauv., *Mariscus* R.Br., *Kyllinga* Rottb. and *Torulinum* Desv. which were given sub-generic rank. It is to be regretted that the bulk of Kükenthal's material on which this work was based was destroyed during the second World War. Some duplicates still exist, however, and are available for study mostly in European herbaria.

In the years between these major works and in preparation for them, Kükenthal made other contributions to the knowledge of African, particularly Tropical African, Cyperaceae, but these must be regarded of lesser importance. (Kükenthal 1913–1937).

Since 1936, Levyns (1943–1947) has critically dealt with *Trianoptiles* Fenzl., a genus of three species endemic to the western Cape Province, and has considered certain aspects of *Scirpus*, *Schoenoxiphium* Nees, *Ficinia* and *Tetraria* Beauv., as well as having described new species within some of these genera. In 1950 this author (Levyns, 1950) was responsible for Cyperaceae in Adamson and Salter's *Flora of the Cape Peninsula*.

Nelmes, working at Kew between the years 1937 and 1958, (Nelmes, 1937–1958) described a number of African species new to science. Most of these were Tropical and West, rather than Southern African and included species of *Carex*, in which genus Nelmes was particularly interested. Within Cariceae he contributed facts and ideas relating to phylogeny, that differed from concepts held by previous workers (Nelmes 1952). He also revised the African species of *Coleochloa* Gilly, *Hypolytrum* L. C. Rich. and *Scleria* Berg. (Nelmes 1953–1956).

Recent appraisal of these revisions has shown them to be not without error. Their great importance is that they provide unified, reasonably comprehensive treatments of genera well represented in Africa, that previously had been dealt with only on regional bases. They have also undoubtedly stimulated interest in the Tropical African sedges in particular.

Most recent works on the Cyperaceae of Southern Africa are those of Podlech (1960) who dealt with South West African representatives and Bodard, (1963) who made a first contribution to the revision of *Bulbostylis* Kunth

in Africa. In the last named work Southern African species are named but many have not been critically dealt with.

In the course of this review it must have become obvious that in dealing with literature relating to the sedges of Southern Africa, it is impossible and of little advantage, to confine references to the region south of the Zambesi River only. This is at best a convenient arbitrary boundary for the botanist, since many Southern African sedges have a distribution far beyond this river to north and to West Africa and often also to Madagascar, India, S. and Central America, and sometimes to Australia and the East Indies, for many species are cosmopolitan, or at least pan-tropic.

Many difficulties that arise in attempting to identify African sedges at the present time are the outcome of much of the early descriptive work having been undertaken on a regional basis, without due consideration for names already applied in adjacent territories, and with no regard whatever for variation that might occur within a species with continental distribution.

Bearing in mind these facts, from now on any worker on the Southern African sedges must consider literature relating to these plants throughout the continent, and when new species are described, to all other areas from which the genus is known.

In this review it is consequently both relevant and desirable to mention some of the more important works relating to Cyperaceae in other parts of Africa. Ridley (1883) dealt with sedges collected by Welwitsch in Angola. Many of these have subsequently been shown to be widely distributed in Eastern Africa where, in some cases, they were already known by earlier names.

De Wildeman (1926-27) described many new species from the Belgian Congo. Not all of these are still maintained, for this author did not check thoroughly against taxa previously described for Africa. During the course of modern continental surveys which, as Bodard (1963) has pointed out, are extremely necessary, more of these species will come under critical consideration. Peter (1936-38) described specimens from Tanganyika. In 1936 was also published the second volume of *Flora of West Tropical Africa* in which Hutchinson (1936) dealt with the Cyperaceae of this part of Africa. This work is now under revision at the Royal Botanic Gardens, Kew. Nelves and Baldwin, (1952) in a short paper containing several illustrations, considered the sedges of Liberia and provided keys for their identification.

Useful keys and many illustrations are also provided in Tournay's treatment of the Cyperaceae of the National Albert Park (Robyns and Tournay, 1955).

Workers on tropical African sedges, if their studies are to be critical, will undoubtedly find their attention drawn to literature relating to Cyperaceae of other continents, for strong affinities undoubtedly exist between Tropical African sedges and those of some other parts of the world, Madagascar in particular.